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BULLETIN

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Vol. 43 No. 10

BULLETIN

OF THE

TORREY BOTANICAL CLUB

OCTOBER, 1916

Fertilization in Fritillaria pudica

KARL SAX

(WITH PLATES 27–29 AND THREE TEXT-FIGURES)

Fertilization in the Angiosperms and especially in the Liliaceae has been the subject of research of many botanists. Yet it is surprising how incomplete and fragmentary is our knowledge of this important and interesting process.

Strasburger (13) in 1884 described fertilization in *Monotropa Hypopitys*. He observed the streaming of the cytoplasm in the embryo sac in the living condition and suggested that the male nucleus was carried to the egg by cytoplasmic streaming.

Guignard (4) in 1891 described fertilization in *Lilium Martagon* and showed a large number of fertilization stages.

In 1897 Mottier (8) first described the vermiform shape of the male nuclei in *Lilium Martagon*.

In 1899 Guignard (5) and Nawaschin (10) published independently their discovery of double fertilization in *Lilium* and *Fritillaria*.

Nawaschin (10, 11, 12) has described fertilization in *Lilium Martagon*, *Fritillaria tenella*, *Juglans nigra* and *Helianthus annuus*. In *Lilium Martagon* and *Fritillaria tenella* he describes the vermiform male nuclei and concludes that they are motile. He maintains that the male nuclei are discharged into the space between the egg apparatus and the "Endospermanlage," whence they make their way to the egg and polar nucleus. He believes that the male nuclei must be motile in order to pass from one

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medium to another and to penetrate the membranes of the egg cell and the "Endospermanlage." In one case he finds the male nuclei linked together and attacks Strasburger's (13) theory of cytoplasmic streaming on the ground that streaming could not carry these nuclei in different directions. He also notes that the bodies, the "X-Körper," which accompany the male nuclei in the pollen tube, are not carried with the male nuclei toward the egg or upper polar nucleus. He suggests that in *Helianthus annuus* one synergid penetrates the embryo sac and pours its contents into the micropyle canal and thereby aids in the entrance of the pollen tube. The cases of fertilization found were apparently few.

In 1900 Guignard (6) published his paper on fertilization in the tulip. He describes the male nuclei in the pollen tube as being of curved shape and of almost homogeneous structure. On leaving the tube they are accompanied by a dense granular substance. The pollen tube closes after the male nuclei escape.

Blackman and Welsford (1) in 1913, working on *Lilium Martagon* and *L. auratum*, describe and picture vermiform male nuclei both in the contents of the pollen tube and attached to the egg and polar nuclei. They also mention and show the two dark bodies in the end of the pollen tube. The male nuclei pictured are long vermiform and often pointed at one end, and their contents are arranged in a rather regular network. The authors maintain that the first male nucleus is smaller and suggest that, since the smaller male nucleus is found in contact with the egg, the first male nucleus goes to the egg. They also believe that the male nuclei are motile.

Welsford (14) believes that the "X-Körper" of Nawaschin are the disintegrating cytoplasm which surrounded the male nuclei. Mention is also made that the pollen tube itself enters the embryo sac before the discharge of the contents.

Other writers have published more or less complete descriptions of fertilization in various Angiosperms. But nowhere is there so complete a description of fertilization in the Angiosperms as has been published by Miss Ferguson (2, 3) and others for the Gymnosperms. Miss Ferguson describes a complete series of egg and sperm fusions in *Pinus strobus* and finds the interesting fact

that the sexual nuclei do not completely fuse but form independent spindles in close proximity to each other.

The material for the present study was collected near Pullman, Washington, in April and May, 1914 and 1915. *Fritillaria pudica* Spreng. is exceptionally good for the study of the process of fertilization because it seeds so freely. In many ovaries practically every sac contained a stage in fertilization. In several ovaries stages were found from synapsis of the megaspore mother cell to stages in fertilization. In the material cut and stained I have found not less than two thousand cases of double fertilization at various stages.

Strong chrom-acetic acid and Flemming's stronger solution were used as fixatives. Most of the sections were cut 10 μ thick, but a few were cut 15 μ and 20 μ. They were stained with modifications of Flemming's triple stain and with safranin and Lichtgrün. Good results were obtained with all stains used.

Although the development of the ovule has been traced from the stage containing the megaspore mother cell up to the time when the young embryo and endosperm are formed, this paper will deal largely with fertilization. Other processes of interest will be dealt with in a later paper.

The mature embryo sac of *Fritillaria pudica* contains the egg and two synergids at the micropylar end, and one normal antipodal cell and one which is disorganized at the chalazal end. Between these groups of cells is the "Endospermanlage" of Nawaschin, which contains the two polar nuclei, the upper one near the egg apparatus, the lower one near the antipodal end. There are thus usually but seven nuclei in the mature embryo sac. The one nearest the chalazal end is at least partly disorganized. The lowest of the four nuclei resulting from the second division usually fails to divide. The three cells of the egg apparatus are somewhat pear-shaped and arranged symmetrically in the upper end of the sac. They are usually very much alike in size and appearance and it is very doubtful if the egg can be distinguished from the other two cells until the time of fertilization. They are bounded by very delicate membranes,

which shows them to be distinct cells. Their cytoplasmic contents are less dense and stain lighter than those of the "Endospermanlage" and antipodal cells. At each end of the "Endospermanlage" is a distinct membrane. At the micropylar end the " Endospermanlage " may project up between or around the cells of the egg apparatus. There is a great deal of variation in this respect, the "Endospermanlage" extending up around the cells of the egg apparatus at different points to varying distances. The upper polar nucleus is smaller and less regular in outline than the lower one. It is always located near the periphery of the sac and surrounded by less cytoplasm. The central portion of the " Endospermanlage " consists of a large vacuole and a thin peripheral layer of cytoplasm. The thickness of this layer is considerably less than the upper polar nucleus (TEXT FIG. 1).

FIG. 1. Mature embryo sac showing: the egg apparatus, one cell of which is only partly visible; the "Endospermanlage" containing the two polar nuclei, the upper one near the egg apparatus; one normal antipodal cell and one which is disorganizing.

Only one case was observed where the tube had reached the embryo sac but had not penetrated it. The tip of the tube was enlarged and rounded and had turned along the nucellus towards one of the nuclei of egg apparatus, probably that of a synergid. In practically all cases one of the synergids is destroyed by the entering pollen tube; but just what the relationship between the synergid and the pollen tube is could not be determined. In one case the cell as well as the nucleus in it, through which the pollen tube is about to enter, has a pointed end towards the end of the pollen tube. But two, or even all of the cells and nuclei of the egg apparatus, may be more or less pointed towards the micropyle. When the pollen tube is in contact with the embryo sac, the cells of the egg apparatus are all intact and show no signs of having emptied their contents into the micropyle, or even of having penetrated the wall of the embryo sac.

In most cases the pollen tube enters the embryo sac somewhat from the side after turning from the micropyle, but sometimes it penetrates the nucellus and embryo sac directly from the micropyle.

The pollen tube just after entering the embryo sac is rounded and swollen at the tip. Only one case was found at this stage but it was well fixed, very clearly stained and apparently normal. The pollen tube and embryo sac are cut longitudinally. The pollen tube contains the two male nuclei. They stain darkly and are much elongated. Two other nuclei are also seen in the sections of the tube. The male nucleus (*a*) nearest the tip shows in FIGS. 3A and 3B. It is long and much coiled and consequently cut across at several places. The second male nucleus (*b*) is seen mostly in FIG. 3C, but the ends of the nucleus are seen in FIG. 3B. This male nucleus is not so long and coiled as the other. The second male nucleus and perhaps the first one are somewhat pointed at the end. The contents at this stage are in an irregular network which takes a deep red stain with saffranin. The chromatin is not entirely peripheral as is shown where the male nuclei are seen in section. To the right in FIG. 3C is a nucleus (*d*) of practically the same size, shape and appearance as the synergid nuclei. The nucleus of the synergid into which the pollen tube has passed, is not found elsewhere in the embryo sac. To the left in FIG. 3C is a second vegetative nucleus (*c*) which is flattened and irregular in shape and situated between the two male nuclei. Portions of these vegetative nuclei are seen in FIG. 3B. FIG. 3A contains some dark-staining granules. The pollen tube did not stain nearly as darkly as others in the same ovary where the male nuclei had already escaped. It is questionable whether both of the vegetative nuclei, (*c*) and (*d*), are tube nuclei, or whether the one to the right (*d*) is the synergid nucleus which has been surrounded by the pollen tube.

The examples of stages in fertilization described so far are comparatively few. But after the male nuclei leave the pollen tube, numerous examples of the stages are found. Not less than eighty male nuclei were found free in the cytoplasm of the cells of the embryo sac, and typical cases of these are figured.

On leaving the pollen tube the male nuclei apparently retain

their curved or coiled shape for some time and in many instances it is probable that they never lose their coiled or curved shape during migration. When the male nucleus escapes near the nucleus with which it is about to fuse, which is always true in the case of the egg, it is probable that it seldom loses its coiled shape, although cases were observed where it was practically straightened out. The male nucleus going to the upper polar nucleus is more frequently straightened out than is the case with the one going to the egg nucleus, probably due to the greater distance it has to travel.

A clear example of the male nucleus going to the upper polar nucleus is shown in FIG. 2. The upper polar nucleus is at the right of the "Endospermanlage." The free male nucleus is distinctly pointed at one end and is curved in a manner that gives it the appearance of motility. The end toward the upper polar nucleus is larger, rounded and tapers slightly toward the middle, where it forms a short rounded arch, and then curves to one side and tapers to a point.

FIG. 1 shows almost all of the contents of the upper end of the embryo sac. The pollen tube is seen entering at one side after turning from the micropyle along the outer wall of the nucellus. It contains two red bodies, the "X-Körper" of Nawaschin, in a disorganized condition. The tube is badly ruptured just below the tip. To the right of the pollen tube is the egg nucleus. One male nucleus is just out of the pollen tube and is partly under the egg nucleus. It is curved and is of about the same thickness throughout. At the lower right side of the figure, the upper polar nucleus is seen. Between the egg nucleus and the polar nucleus is a synergid. The long slightly curved male nucleus is seen in the cytoplasm of the "Endospermanlage." It is smaller at the ends but does not have such an appearance of motility as the male nucleus shown in FIG. 2.

FIG. 5 shows a slightly curved male nucleus in the cytoplasm of the "Endospermanlage" almost in contact with the upper polar nucleus. It is slightly curved and tapers back somewhat from the end nearer the polar nucleus. Both ends are rounded. A male nucleus at practically the same stage is shown in FIG. 7. FIG. 6 represents a rather unusual case of this stage. The male

nucleus is twisted, and much coiled, and is small at both ends. The end to the left is nearer the polar nucleus and curves beneath the thick central portion.

The contents of all of the male nuclei which are free in the cytoplasm of the cells of the embryo sac show great similarity. A typical, very distinct example is shown in FIG. 7. The chromatin contents are in an irregular network. Usually somewhat larger chromatin granules are present in the network in the central portion of the male nucleus (FIGS. 1, 6, 7). There are apparently no nucleoli to be seen at this stage. The male nuclei stain darker than other nuclei of the sac with the stains used.

After the male nuclei are discharged, there are usually two dark staining bodies to be seen in the end of the pollen tube. These bodies, the "X-Körper" of Nawaschin, often show structure and appear to be more or less disorganized nuclei, but in some instances one or both are entirely lacking in structure. They are of various shapes. Usually, however, one is nearly spherical while the other is larger, ovoid, and often pointed at one end (FIG. 9). In this figure the bodies also show definite nuclear structure. They persist throughout all stages of fertilization and even in young embryo development. That these bodies are nuclei can hardly be questioned. They are probably the two vegetative nuclei corresponding to the vegetative nuclei, (*c*) and (*d*), in FIGS. 3B and 3C.

The male nucleus, when in contact with the egg nucleus, is usually coiled or curved. In some few cases, however, the male nucleus is straightened out when it first comes in contact with the egg nucleus. FIG. 4 shows a long tapering male nucleus with the large end touching the egg nucleus. FIG. 8 shows a male nucleus with the large end in contact with the egg nucleus. Many cases of these examples have been observed and usually the male nucleus is larger at the point of contact with the egg.

Whether the male nucleus reaches the egg nucleus while straightened out or coiled, sooner or later it becomes more or less curved around one side of the egg nucleus. FIGS. 10, 11, 12 and 13 show the male nucleus partly curved around the egg nucleus. In FIG. 13, the side of the egg nucleus is somewhat indented where the male nucleus is in contact. This is not uncommon.

The male nuclei finally lose their long curved shape. They contract somewhat, becoming shorter and more rounded in contact with the egg. In some cases the male nucleus seems to occupy an indentation in the egg (FIG. 15), while in other cases the two sexual nuclei are flattened at the point of contact (FIGS. 16, 17). The male nucleus, on losing its vermiform shape, also loses the fine irregular network of its chromatin contents, characteristic of earlier stages. FIG. 14 shows this condition. The male nucleus has contracted somewhat and its contents consist of large and small granules with some of its earlier net-like structure. The egg nucleus is slightly indented. The chromatin granules of the male nucleus become coarser with finer threads running out from them. Many small pieces of chromatin are also to be seen. A little later in some cases nucleoli appear to be present. FIG. 15 shows the male nucleus after it has lost most of its earlier structure, in an indentation in the egg nucleus. FIG. 16 shows a little later stage than FIG. 15, but with the male and female nuclei flattened at the point of contact. In both cases, the male nucleus stains a little darker. The egg nucleus has very large chromatin granules. In FIG. 16, the male nucleus has very small pieces of chromatin along their common boundary. The male and egg nuclei remain in contact a long while before their common boundary finally disappears and their contents mingle. FIG. 17 shows the male and egg nucleus in contact, each containing a large mass of chromatin and small nucleoli. In FIG. 18 the fusion is almost complete. Most of the contents of the male nucleus are in a thread-like structure. Some of the contents of the egg nucleus are thread-like, but a large part are massed in the center of the nucleus. A large nucleolus is present. The thread-like structure appears to run from one nucleus into the other. In both FIGS. 17 and 18, the male nucleus is smaller than the egg nucleus. FIG. 19 shows a stage where the common boundary has disappeared, the contents have apparently mingled, and those from the male and female nuclei are not to be distinguished, but there is still an indication of the outlines of the two nuclei. A similar stage is shown in FIG. 20. In this case the chromatin contents of the fused nuclei are more irregular.

In most cases it is not until the male nucleus and the egg

nucleus have completely fused that we find any appearance of the formation of the spireme. In rare cases, however, the spireme stage is found while the two nuclei are still distinct in outline. A very clear example of this condition is shown in FIG. 21. The spireme thread is rather thick in both nuclei and small nucleoli are still present. It is possible that the nuclear walls have broken down at the point of contact but the nuclei appear to be quite distinct.

Soon after the complete fusion of the egg and the male nucleus, the resulting nucleus becomes more nearly spherical in shape. A spireme is formed. FIG. 22 shows the pear-shaped egg cell with the early spireme of the fertilized egg. The chromatin of the male and female nuclei cannot be distinguished. Delicate threads can be seen at places along the spireme. The thread shortens and thickens until it appears as shown in FIG. 23. Here the spireme is in a late stage—just before the chromosomes are formed. The division of the fertilized egg is normal as is shown in FIGS. 24 and 25. The spindle shows plainly in most cases (FIG. 24), but sometimes it stains lightly (FIG. 25). The figures do not show the entire dividing nuclei but are drawn from sections of the same.

FIG. 25 represents a condition of the egg cell which is characteristic for this and later stages as well as many earlier stages. The egg cell elongates after fertilization. A large vacuole usually forms in the upper part. The fusing sexual nuclei before and after fusion are located in the lower part—lying in a dense cytoplasm. A longitudinal section of the cell shows a more or less crescent-shaped mass of dense cytoplasm, which is well shown in FIGS. 19 and 25.

The two-nucleate embryo is shown in FIG. 26. After division, a definite wall is formed, making two cells, which also appear somewhat crescent-shaped in section. The nuclei are flattened, the short diameter corresponding to that of the cells.

The fusion of the second male nucleus and the two polar nuclei has also been studied. The male nucleus first comes in contact with the upper polar nucleus and together these nuclei migrate to the lower polar nucleus. When the male nucleus comes in contact with the upper polar nucleus, it is usually more or less straightened out. FIG. 27 shows the male nucleus curved along

one side of the upper polar nucleus. Several cases were observed where the male nucleus had both ends in contact with the upper polar nucleus (FIG. 29). Sometimes the male nucleus appears to have come in contact with the upper polar nucleus while still coiled. The male nucleus soon shortens and thickens along one side of the polar nucleus (FIG. 28). The contents of the male nucleus are denser and in larger pieces. The polar nucleus is not indented as is often the case of the egg, but often becomes flattened at the point of contact.

FIG. 2. Embryo sac showing: one male nucleus in contact with the egg nucleus; the other male nucleus and upper polar nucleus in contact and migrating toward the lower polar nucleus.

The contraction and loss of the vermiform shape of the male nucleus usually occurs before the two nuclei migrate to the lower polar nucleus. The male nucleus may, however, retain its vermiform shape during the time of its migration with the upper polar nucleus, or even after the two nuclei have reached the lower polar nucleus. TEXT FIG. 2 shows a longitudinal section of the entire embryo sac with the egg and one of the male nuclei in contact, a synergid, the upper polar nucleus and the second male nucleus in contact, beginning their migration towards the lower polar nucleus, and the antipodal nuclei. The male nucleus in contact with the upper polar nucleus has lost its vermiform shape. The cytoplasm of the upper part of the "Endospermanlage" is massed mostly along one side of the sac and especially around the two migrating nuclei. The strands of cytoplasm and the massing of the contents largely along the one side of the "Endospermanlage" at the upper end is very characteristic.

FIG. 31 shows the migrating nuclei almost in contact with the lower polar nucleus. The male nucleus is on the side nearest the lower polar nucleus and has retained its net-like structure.

Both polar nuclei appear to be in a resting condition. The male nucleus may be attached on any side of the upper polar nucleus.

The cases of migration of the upper polar nucleus together with the male nucleus were not found frequently, only forty-seven cases being found in the great number of fertilization stages. However, the cases of triple fusion of the polar nuclei and male nucleus were very abundant.

TEXT FIG. 3 shows the embryo sac in longitudinal section with a synergid, the egg and male nucleus in contact, and the two polar nuclei and second male nucleus in contact. The male nucleus stains darker and is between the polar nuclei. It will be noted that there is very little cytoplasm in the upper end of the "Endospermanlage" at this time, which is very characteristic. It might appear, on comparing TEXT FIGS. 2 and 3, that the lower polar nucleus migrates also to meet the two approaching nuclei, but if there is a migration of the lower polar nucleus, it is slight, as has been observed in numerous examples, and it is accidental that the two sacs drawn should differ so markedly in this respect.

FIG. 3. Embryo sac showing: the remaining synergid; one of the male nuclei coiled and in contact with the egg nucleus; the other male nucleus and upper polar nucleus just reaching the lower polar nucleus.

FIGS. 33 and 34 show triple fusion. In FIG. 34, the male nucleus is at the side, while in FIG. 33, it is between the two polar nuclei. At this stage the chromatin of the male nucleus has lost some of its net-like structure and contains large pieces of chromatin with delicate threads, and in some cases, nucleoli. FIG. 32 shows a case where the two polar nuclei and male nucleus are in contact, but the latter is still vermiform and its contents are in a net-like structure.

The polar nuclei remain in contact without fusing for considerable time. At the time of fusion the chromatin contents

are partly thread-like with large irregular pieces of chromatin scattered throughout. FIGS. 35, 36 and 37 show the three nuclei completely fused. In FIG. 37, the outlines of the three nuclei can be seen but their common membranes have disappeared. A fine network is to be noted in the central part of the fused nuclei.

Many cases of complete fusion were observed. There is no question but that the two polar nuclei and the male nucleus completely fuse and that no chromatin is thrown out in the process.

The duration of the spireme must be very short, as only a few very clear spireme stages of the triple fusion, or endosperm nucleus, were found. A clear example of a late spireme stage is shown in FIG. 38. There is an irregular nucleolar mass to the left. At this stage the thread is thickened and apparently approximately equally distributed throughout the nuclear cavity. The thread is just beginning to form chromosomes. The nuclear membrane has disappeared and delicate strands of cytoplasm are in contact with the forming chromosomes.

The cases of first division of the endosperm nucleus were abundant and in every case appeared to be normal, apparently an equal number of chromosomes going to each pole. FIG. 39 shows a very clear anaphase of the first division of the endosperm nucleus. The spindle is very clear in this and most other cases. The spindle is pointed at both ends. The first division of the endosperm nucleus results in the formation of two free nuclei. These divide rapidly and often the four or six nucleate endosperm is formed before the egg and male nuclei are completely fused.

Aberrant fertilizations are occasionally encountered. In three cases both the egg and the remaining synergid were being fertilized. The male nuclei were still distinct. In two of these cases the upper polar nucleus was in its usual position near the egg apparatus, but unfertilized. In the third case the upper polar nucleus had almost reached the lower polar nucleus, having migrated alone.

Two cases were observed where two pollen tubes had entered the ovule, one coming down the micropyle, the other entering the ovule at about the level of the egg apparatus. Only the pollen tube coming down the micropyle had entered the embryo sac.

Besides the fertilization of the egg and polar nucleus there

are other processes of interest. Many cases were observed where the contents of the nucleus of the remaining synergid were in the spireme stage. Other stages in the division of the synergid as well as the two-celled stage were observed. No stage of development beyond the two-celled stage was observed.

Several stages were found where the normal antipodal nucleus was dividing. It will be interesting to follow the development of the dividing synergid and the antipodal nucleus through later stages of embryo and endosperm development.

It was noted that the embryo sac becomes longer and curved as it develops. In some stages of early embryo development, it is bent at almost right angles.

DISCUSSION

The cases of the entrance of the pollen tube into the embryo sac, although few, throw some light on problems relating to this process. There is no evidence in *Fritillaria pudica* to show that the synergid empties its contents into the micropyle in order to aid in the entrance of the pollen tube, as has been suggested by several writers. The fact that all the cells of the egg apparatus are intact at the time the tip of the pollen tube is in contact with the wall of the embryo sac excludes such possibilities in *Fritillaria pudica*.

The pollen tube turns along the nucellus and apparently is attracted as close as possible to the nucleus of a synergid before entering. One synergid is practically always destroyed by the entering pollen tube. The suggestion lies close at hand that the synergid is a factor in attracting the pollen tube. The suggestion that the synergid, or parts of it, are used as food by the pollen tube, seems quite tenable.

It is practically certain that in *Fritillaria pudica* the "X-Körper" of Nawaschin are more or less disorganized nuclei. They may be two tube nuclei, but whether there are two tube nuclei formed here has not been determined. Or one of the red bodies may be the disintegrating nucleus of the synergid through which the pollen tube has passed. At all events it is clear that the "X-Körper" of Nawaschin are more or less disorganized nuclei, and not disintegrating masses of cytoplasm from which

the male nuclei have escaped, as Welsford (14) has maintained is the case in *Lilium*.

The male nuclei while free in the cytoplasm of the cells of the embryo sac usually do not have the appearance of motility (FIGS. 1, 5, 7). However, the vermiform appearance of some of the male nuclei while free in the cytoplasm and in contact with the female nuclei, is certainly suggestive of motility (FIGS. 1, 2, 6, 11, 13, 27, 30). It has been noted that the male nuclei, while in the pollen tube, are more or less coiled. Yet when seen part way to the nuclei with which they fuse, especially when the distances are long, the male nuclei are quite straight. The uncoiling is also slightly suggestive of motility. The male nuclei in contact with the egg and polar nuclei are seen to curve around the latter, which suggests independent motility and movement on the part of the male nuclei. The large number of stages found at this time as well as the appearance of the male nuclei, suggests that their movement may be rather slow, perhaps a creeping amoeboid motion. It might be suggested that it is possible that the male nuclei may be conveyed to the nuclei with which they fuse, both by their own motility and by the streaming of the cytoplasm.

It is quite certain that the upper polar nucleus and male nucleus in contact, migrate to the lower polar nucleus by cytoplasmic streaming. In most cases the male nucleus has lost its vermiform appearance before migration. Moreover, it is found in contact at any side of the upper polar nucleus. The accumulation of cytoplasm around the migrating nuclei and the small amount left in the upper portion of the "Endospermanlage" at the time of triple fusion, is evidence that the two nuclei are very probably carried by cytoplasmic streaming (TEXT FIGS. 2, 3).

It has been suggested that the rapidity of movement of the male nuclei is evidence of their motility. Yet the migration of the upper polar nucleus with the male nucleus, which appears to be brought about by streaming, even though the latter have further to go, is observed quite as rarely as free male nuclei.

The abundance of material showing the various stages leading to the complete fusion of the male and female nuclei, as well as the numerous examples of complete fusion and subsequent stages

in the division of the fertilized egg, leaves no doubt that at least in *Fritillaria pudica* the complete union of the male and female nuclei actually occurs. The rare appearance of such cases as that of the spireme stage in the egg and male nuclei when their outlines are still distinct, is probably of little significance in this respect. It is probable that these nuclei subsequently fuse completely because no later stages of incomplete fusion were found. If the adjacent walls of these two nuclei are not broken down, it would suggest that the fusion of the two sexual nuclei is not necessary to stimulate the formation of the early stages in division. This suggestion is supported by cases found in the Gymnosperms by Miss Ferguson and others.

From the many stages and abundant cases of triple fusion, there is no doubt that the two polar nuclei and the male nucleus fuse completely and that the subsequent division is normal. In this fusion there are at least twice as many female as male chromosomes. If this phenomenon of a normal triple fusion holds true for plants whose hybrids show a Mendelian ratio in endosperm characters, then an interesting question arises as to the distribution of the characters among the chromosomes.

SUMMARY

The results obtained from the study of fertilization in *Fritillaria pudica* may be summarized as follows:

1. In the mature embryo sac of *Fritillaria pudica* the egg cell cannot be distinguished from the other two cells of the egg apparatus. The "Endospermanlage" extends up between and around the cells of the egg apparatus.

2. The pollen tube usually turns along the outer wall of the nucellus or embryo sac before entering. At this time the cells of the egg apparatus are all intact.

3. The pollen tube practically always enters and at least partly destroys one synergid.

4. Although a distinct appearance of motility is evident in many male nuclei, the majority do not suggest much motility.

5. The male nucleus and the egg nucleus fuse completely before division.

6. The upper polar nucleus, with the male nucleus in contact

with it, migrates to the lower one, probably by cytoplasmic streaming.

7. The two polar nuclei and male nucleus fuse completely and the subsequent division is normal.

8. The two red bodies, the "X-Körper" of Nawaschin, which remain in the pollen tube after the male nuclei have been discharged, are very probably nuclei. They probably correspond to the two vegetative nuclei described in the pollen tube before the two male nuclei were discharged.

In conclusion I wish to acknowledge my indebtedness to Dr. C. E. Allen for literature, to Dr. F. L. Pickett for extending the privileges of his laboratory, and especially am I indebted to my wife, Dr. Hally Jolivette Sax, for her constant encouragement and assistance throughout the work.

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Explanation of plates 27–29

All drawings were made with the aid of the camera lucida. All figures were drawn from single sections. The magnification is as follows: FIG. 8, 520 diameters; FIGS. 1, 30–39, 720 diameters; FIG. 2, 750 diameters; FIGS. 3–7, 9, 10–29, 1,120 diameters.

PLATE 27

FIG. 1. Micropylar end of the embryo sac in section, showing entrance of pollen tube, with disorganized red bodies—a portion of one synergid—one male nucleus coming in contact with the egg nucleus on the under side, and the second male nucleus in the cytoplasm of the "Endospermanlage" on its way to the upper polar nucleus.

FIG. 2. Section of upper part of embryo sac showing one of the male nuclei on way to polar nucleus.

FIGS. 3*A*, 3*B*, 3*C*. Consecutive longitudinal sections of a pollen tube after entering the embryo sac. The two male nuclei, (*a*) and (*b*), stain darker than the vegetative nuclei. Two vegetative nuclei are shown, (*c*) and (*d*).

FIG. 4. Male nucleus coming in contact with the egg nucleus.

FIG. 5. Male nucleus almost to upper polar nucleus.

FIG. 6. Male nucleus coiled and twisted, on way to upper polar nucleus.

FIG. 7. Male nucleus on way to upper polar nucleus.

FIG. 8. Male nucleus touching the egg nucleus.

FIG. 9. Pollen tube containing the two dark bodies which show nuclear structure.

FIG. 10. Male nucleus coiled and in contact with the egg nucleus.

FIG. 11. Male nucleus in contact with egg nucleus.

PLATE 28

FIGS. 12, 13. Male nucleus in contact with egg nucleus.

FIG. 14. A later stage. The male nucleus has lost its vermiform shape and its earlier net-like structure.

FIG. 15. Male nucleus in indentation of egg nucleus.

FIGS. 16, 17, 18. Male nucleus and egg nucleus fusing.

FIG. 19. Egg cell with male nucleus and egg nucleus completely fused.

FIG. 20. Complete fusion of egg and male nucleus.

FIG. 21. Case of formation of spireme before complete fusion.

FIG. 22. Egg cell containing the fertilized egg in early spireme.

FIG. 23. Egg cell containing the fertilized egg in late spireme.

FIG. 24. Equatorial plate stage in first division of fertilized egg.

FIG. 25. Typical crescent-shaped section of the equatorial plate stage of dividing fertilized egg cell.

FIG. 26. Two-nucleate stage of embryo.

PLATE 29

FIG. 27. Male nucleus in contact with upper polar nucleus.

FIG. 28. A slightly later stage than Fig. 27.

FIG. 29. Male nucleus with both ends in contact with upper polar nucleus.

FIG. 30. Male nucleus in contact with upper polar nucleus while on way to lower polar nucleus.

FIG. 31. Male nucleus and upper polar nucleus almost touching the lower polar nucleus.

FIG. 32. Two polar nuclei and coiled male nucleus in contact.

FIG. 33. Triple fusion. Male nucleus between the polar nuclei.

FIG. 34. Later stage of triple fusion with male nucleus on the side.

FIGS. 35, 36, 37. Endosperm nucleus resulting from the complete fusion of male nucleus and polar nuclei.

FIG. 38. Late spireme stage of endosperm nucleus.

FIG. 39. Early anaphase of first division of endosperm nucleus.

Additional species of Opuntia

DAVID GRIFFITHS

(WITH PLATE 30)

Plants of the following species have been growing in our collections for the past five to eight years. Some of them have been held under provisional names for a long time in the hope that they might eventually be referred to species already described. They can not, however, be so referred and must receive new names.

Opuntia columbiana sp. nov.

A low, half prostrate species, seldom over 15 cm. high; the distal joints mostly erect, the ones on the ground rooting freely; joints narrowly obovate, about 5 × 15 cm. in last year's growth, at first yellowish to medium light green but the second year becoming decidedly yellowish green, slightly raised at areoles, fragile, and easily broken, making it very difficult to grow plants to maturity; areoles subcircular to obovate, 2 mm. long, enlarging in age and prominent, 2 mm. high on account of the profuse development of wool, light brown; spicules yellow at first, in a compact tuft 1 to 1.5 mm. long in upper part of areole, later, especially the second year, becoming unequal and scattering, and 5 mm. or more in length; spines yellowish to white, centrals one to three with one long, porrect or sloping down 3–4 cm. long and the other one or two 2 cm. long and widely spreading, and commonly three or four about 1 cm. long in the lower angle of the areole tightly recurved, often there are two or three porrect-spreading, long spines, and the others (three short and about two 2 cm. in length) all tightly recurved; flowers light yellow, filaments reddish brown, style white, stigma light green.

This species is apparently confined to the sandy lands along the Columbia and Snake River valleys, and is particularly abundant near Pasco, Washington. The above description applies to my inventory No. 10041, from Pasco, Washington, but the spines vary greatly in color, and associated with this difference in color of the spines is a comparable difference in coloration of the plant body. Specimens collected under my inventory No. 10042 have

darker colored spines; the joints commonly about 4 × 9 cm. and the spines in part brown, especially on apex of joints.

Opuntia cucumiformis sp. nov.

A low, branched, cylindrical-oval-jointed plant, 18 cm. high and 35–50 cm. in diameter; at first yellowish green, turning gray; joints 10 cm. long, 3.5 cm. in diameter, broadly pointed to rounded above, cylindrical, tubercular, raised at areoles, the low, rounded ridge extending downward 1.5–2 cm.; areoles obovate, 2.5 mm. long, gray, rather sunken, 1.5–2 cm. apart, only upper ones armed; leaves conical, ascending, 5 mm. long, slightly flattened on inside; spicules yellowish, at first not visible but at one year of age filling entire areole, which becomes subcircular, the spicules developing in successive lengthening zones from center of pulvinus; spines yellowish, translucent, bone-like, 1–2.5 cm. long, porrect, diverging but slightly, one to five in upper areoles only, not sheathed; flowers deep yellow, lighter within, having faint tinge of red in upper edges, about two rows of petals opening to 4 cm. in diameter; filaments white, style white, stigma white, variable, six-parted, small; bud distinctly reddish tinged at apex which is bluntly pointed and subtended by spicules, 3–5 mm. long, from the marginal areoles of the ovary; fruit oval to obovate, about 16 by 38 mm., deeply pitted at apex with small cavity about 4 by 8 mm. containing numerous small, atrophied ovules, its areoles small and distant below but closer above, bearing around top of ovary one or two yellowish spines 12–15 mm. long, and a small tuft of spicules 4–5 mm. long.

This species has been received from European collections as *Opuntia ciribe* Engelm., a native of the peninsula of Lower California, but it has little relation to that species and in all probability is native to the Cordillera region of South America. Several plants of it have been grown to maturity, but in no case have the fruits, which are produced in considerable abundance, matured seeds. The pulp cavity is always empty and the fruit remains attached to the plants indefinitely.

Opuntia calantha sp. nov.

A low, creeping, prostrate species, 15 cm. high and a meter in spread; joints obovate, sub-pointed above and below, inequilateral, about 4 × 11 cm., tuberculate-wrinkled, mostly deep green; areole small, 1–1.5 mm. long, obovate, at first tawny, turning gray; leaves small, subulate, cuspidate, red, 1 mm. long;

spicules yellow, not prominent at first but later 3–4 mm. long and scarcely distinguishable from the spines, from which they differ only in size and position, and very slightly in color; spines white, short, porrect-divergent, five to ten in number, 5 mm. or less in length with often as many spicules a trifle less divergent in upper portion of areole; flowers carmine, filaments carmine, stigma very deep, dark green, thirteen-parted, with short segments and open throat; fruit, with us, greenish to yellowish, hemispherical, deeply pitted, 1.5 cm. in diameter.

This species is more or less common in European collections, and is probably of South American origin. It is commonly received as *Opuntia microdisca* A. Weber, but differs from that species in almost every diagnostic character. We have had plants of it in blossom for three or four years but in no case have fertile fruits been produced, although hand-pollination has been resorted to and natural pollination by insects has been universal. The reason for this sterility is not apparent, but it may be due to our intense heat and drought during the time that the flowers are open.

Opuntia longiclada sp. nov.

An erect, open-branched shrub a meter or more high and having a spread of 2 m.; joints elliptical, widest slightly below middle and gradually narrowed both ways, pointed above and below, commonly 12 × 36 cm., this season's growth now in blossom commonly 10.5 × 33 cm., at first rather bright yellowish green, turning slightly gray green yet having but little bloom, slightly raised at areoles and this disappearing the second year; areoles gray or light tawny, oval to subcircular, commonly 4 mm. long, bearing a darker central area; spicules inconspicuous, yellow, becoming noticeable and 2 mm. long in a compact, connivent tuft in upper portion of areole at one year of age; spines one to three, 1–1.5 cm. long, yellow, turning white, increasing with age to six to eight and often becoming 3 cm. long, usually one or two on sides of joints and more numerous on edges, flattened, twisted, with translucent tips; flowers yellow, greener within, 5.5 cm. in diameter or 6 cm. when fully opened; turning deeper yellow and developing the faintest tinge of red within at close of day; filaments greenish, style white, stigma large, light green, nine-parted; inner petals nearly orbicular; buds dull light green with tinge of dull red on the upper edges of the sepals; fruit pyriform, purplish red throughout. (PLATE 30.)

This species has been carried in our collections for the past

eight years under S. T. G. No. 2838, and has been grown successfully in two situations in Texas besides Chico, California. It was not known for a long time whether it was hardy or not, consequently we grew it inside at Chico where it produced a moderate crop of fruit and a prolific vegetative growth. In the field, however, its vegetative development is very much curtailed but it is loaded with fruit. It was received originally from some European collections. Since being transferred to Chico it has grown under S. T. G. No. 2838. Its natural habitat is unknown.

Opuntia platynoda sp. nov.

A low, erect to ascending, densely branched, fragile-jointed species, seldom 45 cm. high, but often 60–100 cm. in diameter; joints flattened, small, obovate to mostly fusiform-oblong, 4 × 13 cm. for old joints of this season, but very variable, many joints of last season's growth only 3.5 × 9 cm., dark, glossy green, and darker and often purplish below the areoles, which are slightly raised, tubercular at areoles first season but later entirely smooth, but always more or less darkened in color below them; areoles gray to light tawny, obovate, about 4 mm. long, increasing in age to subcircular; spicules at first inconspicuous in a small tuft in upper portion of areole, but later at two or three years occupying half of the areole, and fading to a light dirty brown or yellowish; spines erect, divergent, at first brown, turning through a mottled condition to white with translucent bone-like tips, flattened, twisted, stout, one to three, seldom four, with lower areoles naked, upper terete spine largest, 2.5–3 cm. in length, and ascending or porrect, the others lateral or situated directly below, besides these often there are two delicate short lower lateral ones, 3 mm. in length in addition; flowers lemon yellow, 4.5–5 cm. wide when fully opened, outer segments greenish red and tightly appressed as is typical of South American forms in the bud; petals tipped with greenish red, obovate, retuse, and minutely cuspidate in the notch; filaments white, style white, stigma white, six-parted, petals about 3 cm. long; fruit pyriform, green with blush of greenish red on one side, or entirely greenish red, with exception of basal portion, large, subcircular, gray to tawny areoles, 12–18 mm. apart, and an occasional short spine.

With us the plant grows very rampant in the sash house, requiring constant pruning to keep it in check. It blossoms very freely in June and July. Up to this time the fruit has been all but sterile, none having over one half dozen mature seeds, but a

great many aborted ones, showing that there is something wrong with the fertilization of the plant in this situation.

The description is drawn from No. 9266 P. I. G., cultivated at Chico, California, from cuttings secured from European collections. I have no definite information of its habitat, but feel certain that it is of South American origin. Its affinity is clearly that of a large group of South American species with short, blunt buds of closely appressed, wide, thick scales, short leaves, and copperized areolar stains. The species is frequently injured by cold weather out-of-doors at Chico, California.

OPUNTIA MICROCARPA Engelm.

A stout, robust, large-jointed, erect species, making a bush 1.5 m. high and 2 m. in spread, with the main lower arms mostly resting on edges or self-supporting, ascending or nearly horizontal; joints large, light bluish, moderately glaucous, often 25 × 35 cm., sharply rounded above, not raised at areoles after first year; areoles variable in size, light brown, obovate, 5–6 mm. long on sides and some 8 mm. on edges of last year's growth, becoming subcircular and black in age; spicules light-brownish yellow, scattered, unequal, 3–10 mm. in length, not especially prominent excepting on margins of joints; spines white, with brown bases of very ununiformly tinted but always dull and dark brown, strongly flattened, twisted, bent and variously curved, variable in number and length, two to six and 1–4 cm. long, increasing in length and numbers in age; flowers large, 9–10 cm. in diameter, yellow with greenish centers, filaments yellow, style greenish to very faintly reddish tinted, stigma large, deep green, ten- to thirteen-parted, coarse; buds rather sharply pointed, olive green with a very faint blush of red in the tips of the outer, lax to recurved sepals; fruit deep purplish red throughout and bearing prominent, tawny areoles, having the usual quota of spicules, rather lighter than those of the plant, and a few fugacious spines 1 cm. long; umbilicus broad, flat to slightly concave.

This is one of the larger, more robust of the southern Arizona species. The description of the spines might be misleading for the general impression which they give is that of white, leaning toward that peculiar translucent aspect common to so many species. It is not at all abundant but occurs commonly in scattering individuals in the foothills at an elevation of about 3,000 feet. This is the first time this species, which was named by Dr. Engel-

mann* from Stanley's figures, has been recognized, although it has a considerable known distribution and is a very characteristic thing. I have seen fine specimens of it in the type locality near Solomonville, Arizona, and at various points to the southwestward. It extends in this direction as far as the Tucson region. I have had it in manuscript under a provisional new name for years from the latter region, but refrained from publishing on account of a suspicion that it might be this species on account of the shape of the joints as shown in the Stanley figures. A careful study of the pears of the type locality leaves no doubt in my mind as to its identity.

Opuntia crystalenia sp. nov.

An erect, tree-like form, 2–2.5 m. high with a distinct cylindrical trunk and tree-like top; joints broadly obovate to nearly subcircular, about 18 × 25 cm., glaucous, blue-green, becoming more yellow after two years of age, at one year about 3 mm. long on sides of joints but enlarging irregularly and becoming subcircular in age, at first tawny but turning gray; leaves small, 4 mm. long, subulate, cuspidate, slightly flattened and becoming somewhat recurved at tip; spicules yellow, in a compact tuft in upper part of areole, not prominent, scarcely protruding from surface of joint, increasing only in occasional areoles in age; spines white, porrect in upper two thirds of joints only, one to three or four, usually two, variable, the longest 10–15 mm. in length and there are usually present one to two or three hair-like, delicate spines besides in the lower angle of the areole; flowers yellow, lighter colored within, filaments yellow above and greenish below, style white, stigma large, conical, dull dark green, ten-parted; buds light, dull greenish red, with a slight grayish, glaucous sheen; fruit subglobose, medium sized, about 4–4.5 cm. in diameter, light red all the way through, flower-scar moderately dished to nearly flat, areoles tawny to brown, about 8 mm. apart and having prominent wool, variable spicules 1–2 mm. in length and four to ten delicate fugacious spines, 4–12 mm. long, tawny brown.

This is a common species both native and in cultivation upon the Mexican highlands and is prized for its edible fruits. The type was collected at Cardenas, Mexico, under my inventory number 8030 in August, 1905. It has been grown in our experimental plantings at Brownsville and San Antonio, Texas, and Chico, California.

* Emory's Recon. Append. 2: 158. 1848.

Opuntia ithypetala sp. nov.

A tall, erect, tree-like, open-branching plant 2 m. high or more with a distinct trunk and widely spreading, ascending to drooping branches; joints large, obovate, contracted below into a long stipitate base, very often 19 × 45 cm., but commonly only 14 × 26 cm., bright dark green, tubercular-raised at the areoles, the surface not becoming flat and smooth for two or three years at least, bright dark green, mostly without bloom; leaves subulate, cuspidate-pointed, slightly flattened, 5–6 mm. long; areoles oval to subcircular and often 1 cm. in diameter, 4–5 cm. apart on sides of joints; spicules not visible; spines white on second year's growth, three to five, mostly three or four, the central one porrect and largest 3–4 cm. long, the lower one short, 1–2 cm. and recurved, the others divergent, flattened, twisted, formidable, increasing on old trunks to six to ten and often becoming 8 cm. long and very stout; flowers light canary yellow, fading to light rose purplish late in the day, the petals erect, not spreading, becoming 3 cm. in diameter when fully opened; filaments white to slightly greenish below and very light pinkish tinted above, style white, stigma very light green, six-parted; buds conical-pointed, light olive with only a tinge of red at the tip, the scales wide and closely appressed; fruit light purplish red, slightly raised tubercular at areoles and deeply pitted, each upper areole bearing mostly 1 white, porrect spine 1 cm. long and occasionally an additional smaller one 3 to 5 mm. long below the big one, the pulp being much deeper purplish red than the outside and brittle with a pleasant touch but not very sweet.

This species was received from the Royal Botanical Garden at Berlin as *Opuntia Hanburyana* A. Weber. It is more closely related to *Opuntia Schumanni* A. Weber but as the description above indicates it is very different from either one. It agrees with the latter in having the petals erect when the flower is fully opened; it does not agree with the former in any particular. It has been grown to maturity very successfully in our two situations in Texas as well as at Chico, California. When first received it was assigned the inventory number of our San Antonio garden, 506, and under this number it has been carried at Chico, California.

Opuntia rubiflora sp. nov.

Plant low, spreading, 30–45 cm. high and having a spread of a meter or more; joints obovate, mostly 12 × 18 cm. in last year's growth, but older ones larger, medium dark green with a little

pruinosity, broadly rounded above and gradually narrowed below into a short stipe; areoles obovate above and subcircular below, about 3–4 mm. long with prominent gray wool the second year; spicules brown on this year's growth, changing to yellow in situ the second year, situated in a compact tuft in upper portion of areole, 2 mm. long; spines white with brown to straw-colored bases, on last year's joints two or three, usually one recurved 1–2 cm. long, white, the others stouter, 3–4 cm. long, white with brown to straw-colored bases, porrect, divergent, flattened, slightly twisted and at times showing a very faint annulation, increasing and becoming six to eight in number and somewhat lengthened in age; bud medium-pointed with loose, narrow scales of an olive green color but with a tinge of dull pinkish red in the upper portion; flowers pink, filaments yellow, greenish below, style white, stigma very light greenish, six-parted, with long-pointed divisions which are cuspidate, the general shape of the stigma being conical.

The species was received originally in the form of cuttings from European collections, designated by an unpublished varietal name under *Opuntia camanchica* Engelm. & Bigel. It is, however, a perfectly good species. Its habitat was not stated.

Opuntia megalantha sp. nov.

A tall, robust, erect, open-branching plant 2 m. or more in height; joints obovate, broadly rounded or often, when young, bluntly pointed above, becoming more rounded the second year, glaucous-gray-green, last year's joints commonly 14 × 21 cm.; areoles at first brown turning gray, variable, oval-obovate to subcircular, enlarging in age, about 3–5 mm. long the first season; spicules yellow, scattered through the edge of the areole, wool 4–5 mm. long, increasing slightly in age but only in scattered places on the plant, usually there is no increase at all but the wool increases or grows anew and the areoles on the old trunks three or more years old often bright brown like new growth, often becoming transversely elongated and 1 cm. in width on old trunks; spines yellow, in some cases slightly tinted at base, some more or less mottled after first year but semi-translucent, dirty yellow in age, one to three, the longest 2.5 cm., increasing to 4–5 cm. in length and four or five in number on old wood; flowers yellow, 10–11 cm. in diameter, petals 5 cm. long, obovate, usually notched at the rounded apex, filaments greenish below and white or yellowish above, style white, stigma large, in rare instances 1 cm. in diameter, white or slightly greenish tinged, flattened by in-curving of points, eight- to nine-parted; fruit dark red throughout

with subcircular areoles 3 mm. in diameter, the upper especially with prominent spicules 3–4 mm. long, merging imperceptibly into the delicate, fugacious spines which may be a cm. long or less.

This species was received from the Royal Botanical Garden at Berlin as *Opuntia Bergeriana* A. Weber, and has been grown with us in two situations in Texas and one in California. In some respects the plant does suggest *Opuntia Bergeriana* but the character of the flowers alone would exclude it from that species. It differs also in general habit, nature of spination and form and character of joints. In the season of 1914 our plants at Chico, California, blossomed profusely and set a good crop of fruit, but in no case did any seed form, the fruit being made up mainly of rind with a very small, empty seed cavity, save for the minute dried ovules. In 1915, however, the earlier fruits did not differ very materially from those of the previous year except that two or three seeds were produced in the fruit; but later crops, blossoming in late June and early July, produced an abundant seed crop. The species is carried in our collections under No. 2825 S. T. G. Its habitat is not known.

UNITED STATES DEPARTMENT OF AGRICULTURE

Explanation of plate 30

OPUNTIA LONGICLADA Griffiths

Terminal joints and flower buds, about half natural size, cultivated at Chico, California.

Cambial activity in certain horticultural plants*

LEWIS KNUDSON

As stated by the writer in a previous publication,† there is a scarcity of data respecting the season of cambial activity in woody plants. This lack of knowledge, particularly with respect to cambial activity in the fruit trees, is the more surprising when one considers its significance to pruning and fertilizer practices, and since ultimately a rational system of fruit culture will be based on an accurate knowledge of the life history of the plant. It was in the hope of supplying some of the desired information that an investigation on this subject was begun in the summer of 1909.‡ It was found impossible to continue the investigation, except for a few observations made in the summer of 1913, but because of the scarcity of data on this subject it seems advisable to record the results of the observations made.

OBSERVATIONS ON THE GRAPE

Methods.—For the investigation a number of vines were selected of the Worden variety (*Vitis labrusca*). They were uniform as regards size and conditions of growth. They had been growing for four years on a plot of land on the campus of Cornell University, Ithaca, New York. The vines were under the care of the Department of Pomology, and had been properly pruned during the previous seasons.

At intervals throughout the season cuttings were taken from the one-year-old wood. These cuttings were removed in all cases from the basal internodes of different shoots and, as far as possible, from shoots of the same exposure and the same diameter. Cuttings from new shoots were likewise made from the basal

* Contribution from the Laboratory of Plant Physiology, Cornell University.

† Observations on the inception, season, and duration of cambium development in the American larch [*Larix laricina* (Du Roi) Koch]. Bull. Torrey Club **40**: 271–293. *pl. 18, 19.* 1913.

‡ The field notes and collection of material were made by Dr. George R. Hill, Jr.

internodes. The material was fixed in Gilson's solution, imbedded in celloidin, and later sectioned and stained. On the same days that material was collected, observations were taken on the external manifestations of growth in order that the formation of xylem and phloem could be correlated with the growth of leaves, elongation of new shoot, and development of fruit.

In TABLE I are given the data on the growth-measurements in the grape.

TABLE I

DIAMETER INCREASE OF PHLOEM AND XYLEM IN ONE-YEAR-OLD SHOOTS OF THE GRAPE

Number of cutting	Date	Diameter of branch, mm.	Increase of xylem, microns	Increase of phloem, microns	Leaf, fruit, and shoot development
4	May 8	3.5	0	0	Buds swelling
12	" 15	4.75	0	0	Largest leaf 2 mm. wide
25	" 23	6	0	0	New shoot 30 cm. long. Largest leaf 11 mm. wide. Fruit-bud cluster 3 cm. long
46	" 29	4.5	102	61	Leaf 16×16 cm. New shoot 60 cm. long. Fruit-bud cluster 6–8 cm. long, not yet open
74	June 7	4.75	0	0	Largest leaves 18×18 cm. New shoot 86 cm. Fruit-bud cluster 5.5 cm. long; some open
94	" 15	5	143	73	Leaf 20×19 cm. New shoot 96 cm. Tendril developing. Axillary shoot 12 cm. long, with leaves 4 cm. broad. Fruit set. Only occasional stamens to be seen
110	" 20	—	102	71	Leaf 20 cm. broad. New shoot 100 cm. Grapes size of peas
144	" 29	6.5	486	222	Leaf 20×20 cm. New shoot 155 cm. Size of berries (largest) 12 mm. diameter
168	July 19		1,000	445	New shoot 195 cm.
185	Aug. 9		980	405	Grapes nearly full-grown, 16 mm. diameter
197	Nov. —		729	405	

Diameter increase began simultaneously in both phloem and xylem. The cambial activity began between May 23 and May 29, at which time the leaves were almost completely developed. Cambial activity ceased before August 9, for at this time the new xylem and the new phloem were completely differentiated and the cambium was in the resting condition. Between July 19 and August 19 a periderm layer was produced, cutting off the old phloem from the new. At the base of the new shoot, at about the same time, a periderm layer developed just outside the phloem, cutting off the entire cortex.

OBSERVATIONS ON THE PEACH

In studying cambial activity in the peach the methods employed were essentially the same as for the grape. Three peach trees were used, all growing under apparently identical conditions on the grounds of Cornell University. The trees were of the variety known as Wakefield and they were probably fifteen years of age. They had produced a good crop of fruit during the preceding season, and the same held true for the year when the observations were made. Cuttings were taken of one-year-old, five-year-old, and ten-year-old branches, the branches being respectively of approximately the same exposure and the same diameter. The detailed data follow in TABLE II.

TABLE II

AVERAGE DIAMETER INCREASE IN THE PEACH

Date of cutting	One-year-old branches		Five-year-old branches		Ten-year-old branches		General notes on growth
	Xylem microns	Phloem microns	Xylem microns	Phloem microns	Xylem microns	Phloem microns	
May 8..	61.5	—	112	92.2	287	102	Buds just opening
" 15..	61.5	49	153	82	184	102	Leaves 4 cm. long. Late blooming period
" 23..	143	114	143	120	205	102	Leaves 9 cm. long. New shoots 2 or 3 cm. in length
" 29..	—	—	225	123	307	123	Leaves 9 cm. long, full-grown. New shoot 6 cm. Fruit 20×10×12 mm.
June 7..	174	94	225	120	410	266	New shoot 9 cm. long. Fruit 22×25×33 mm.
" 1 ..	—	—	246	164	512	307	New buds evident. Fruit 27×30×36 mm.
" 20..	266	116	205	153	584	320	Fruit 38×30×28 mm. Stone just hardened
" 29..	95	69	250	205	500	287	Fruit 40×35×30 mm.
July 19..	166	75	205	164	492	307	Fruit just beginning to ripen
Aug. 9..	145.9	75	266	164	389	205	

An examination of the table reveals the fact that cambial activity began in the peach at the time of the opening of the buds. This is contrary to the condition found in the larch, grape, and apple. Complete differentiation of the new xylem was evident by July 19, when the cambium layer appeared to be in a resting condition. It is not possible to draw conclusions regarding the period of greatest cambial activity, since the variation in growth in the different branches is apparently considerable.

OBSERVATIONS ON THE APPLE

The methods of investigation in the apple were essentially the same as in grape and peach. Only one tree was used. It was growing on the campus at the foot of a four-foot road embankment The tree was about forty years old, and for several years no practical attention had been given it. Cuttings were removed from one-year-old branches, from four-year-old branches and from one of the main branches having a diameter of 4 cm. The detailed data are given in TABLE III.

TABLE III

AVERAGE DIAMETER INCREASE IN THE APPLE

Date of cutting	One-year-old branches		Four-year-old branches		Ten-year old branches		General notes
	Xylem microns	Phloem microns	Xylem microns	Phloem microns	Xylem microns	Phloem microns	
May 8..	32	0	—	—	0	0	Leaves 2.5×1.5 cm. Pink of fruit buds evident.
" 15..	40	0	20	—	123	—	Leaves 2.5×2 cm. Full bloom
" 23..	40	40	100	—	—	—	Leaves 6.5×3 cm. Fruit set
" 29..	150	82	157	133	205	—	Leaves 11×4 cm. Full-grown. Fruit 8 mm. diameter
June 15..	287	98	180	123	246	143	Fruit 18 mm. diameter
" 20..	430	143	246	205	512	185	Fruit 23 mm. diameter
" 29..	686	123	440	125	540	164	New buds appearing. Fruit 36 mm. diameter
July 19..	—	—	594	246	492	164	Fruit 37 mm. diameter
Aug. 9..	379	82	840	205	738	160	
Nov. 4..	594	90.2					

In each case cambial activity began before May 15, but it was impossible to determine from the sections whether or not phloem formation had begun. In all cases xylem formation was completed by July 19 and the characteristic thickening of the cell walls was also practically completed. By August 9, the date of the last observations, the cambium was in its resting condition. The most rapid increase began just after the leaves had attained full size.

INCIDENTAL OBSERVATIONS IN 1913

Material for examination was collected in 1913 from the apple, peach, pear, plum, and cherry. Two apple trees were examined, a Baldwin and a Rhode Island Greening. The trees were about

seventy years of age and were growing in an old orchard. In both cases examination of sections from one-year-old, three-year-old, and five-year-old branches revealed the fact that by July 17 the last few layers of xylem cells were being formed, and sometimes between July 23 and July 30 the xylem and phloem formation was completed and the cells were completely differentiated. The cambium was then in its resting condition. Material was also taken from three-year-old and five-year-old branches of the pear. The tree was about twenty years of age and was growing in a yard. In each case xylem formation was completed by July 17. Incidental observations made on the plum, peach, and cherry on three- and four-year-old branches indicated that xylem formation was complete by July 23 and the cambium was in a resting condition. These trees were bearing trees about twenty years old and were growing in a farmyard.

In concluding, mention should be made of the fact that no evidence was obtained to indicate that phloem formation continued later than xylem formation.

INDEX TO AMERICAN BOTANICAL LITERATURE

1913-1916

The aim of this Index is to include all current botanical literature written by Americans, published in America, or based upon American material; the word America being used in the broadest sense.

Reviews, and papers that relate exclusively to forestry, agriculture, horticulture, manufactured products of vegetable origin, or laboratory methods are not included, and no attempt is made to index the literature of bacteriology. An occasional exception is made in favor of some paper appearing in an American periodical which is devoted wholly to botany. Reprints are not mentioned unless they differ from the original in some important particular. If users of the Index will call the attention of the editor to errors or omissions, their kindness will be appreciated.

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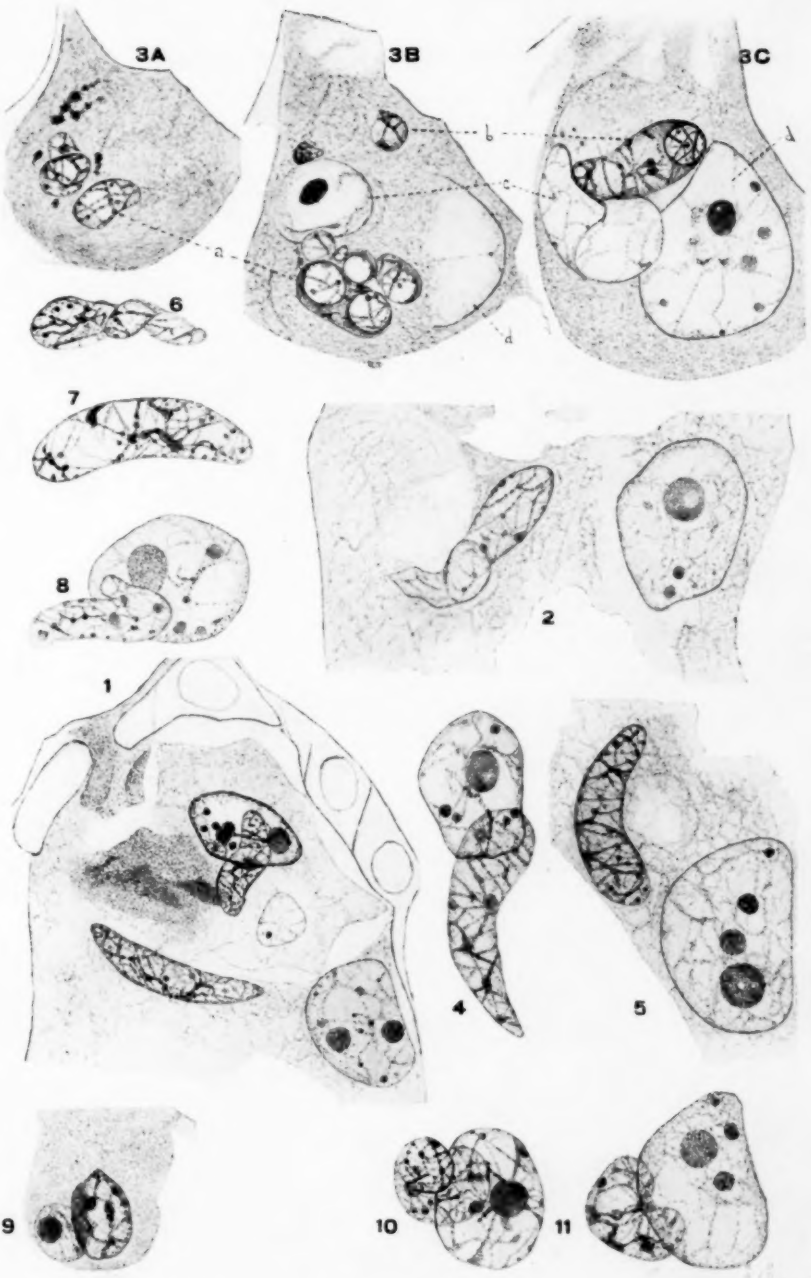

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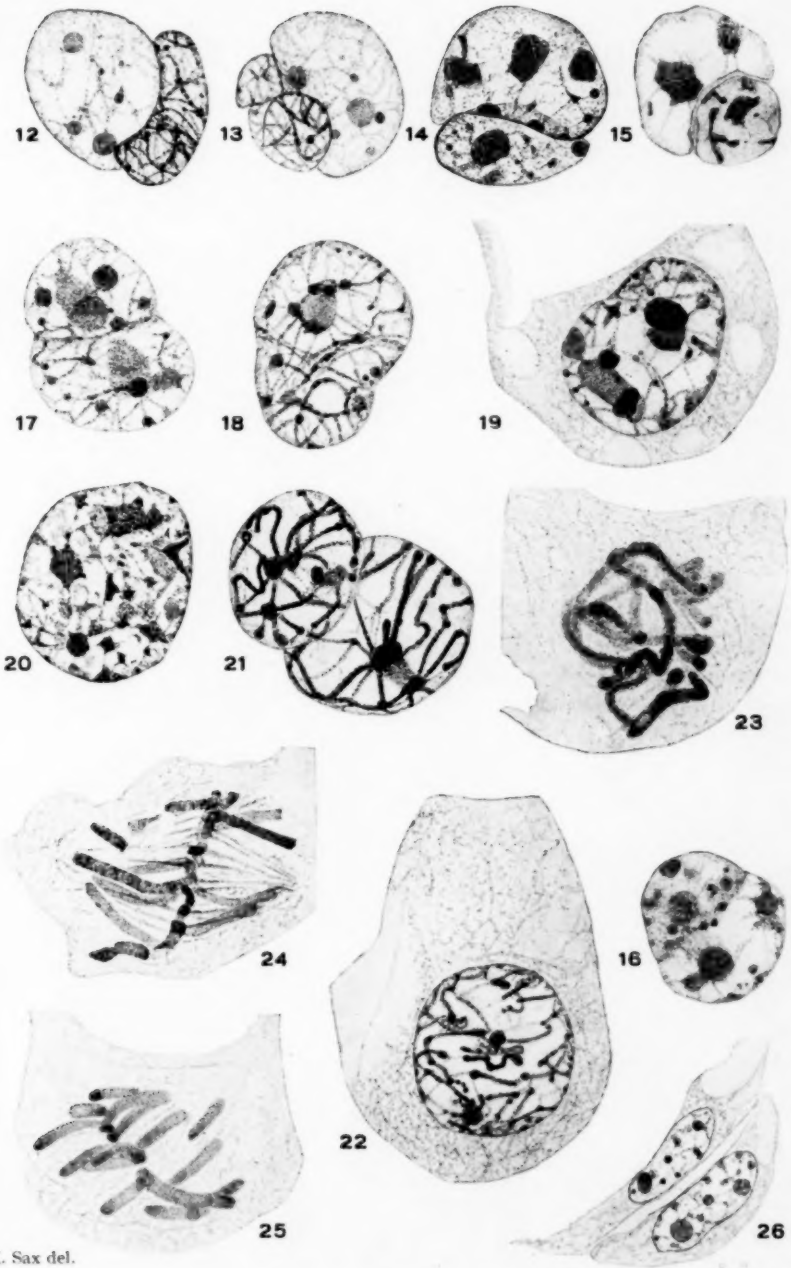

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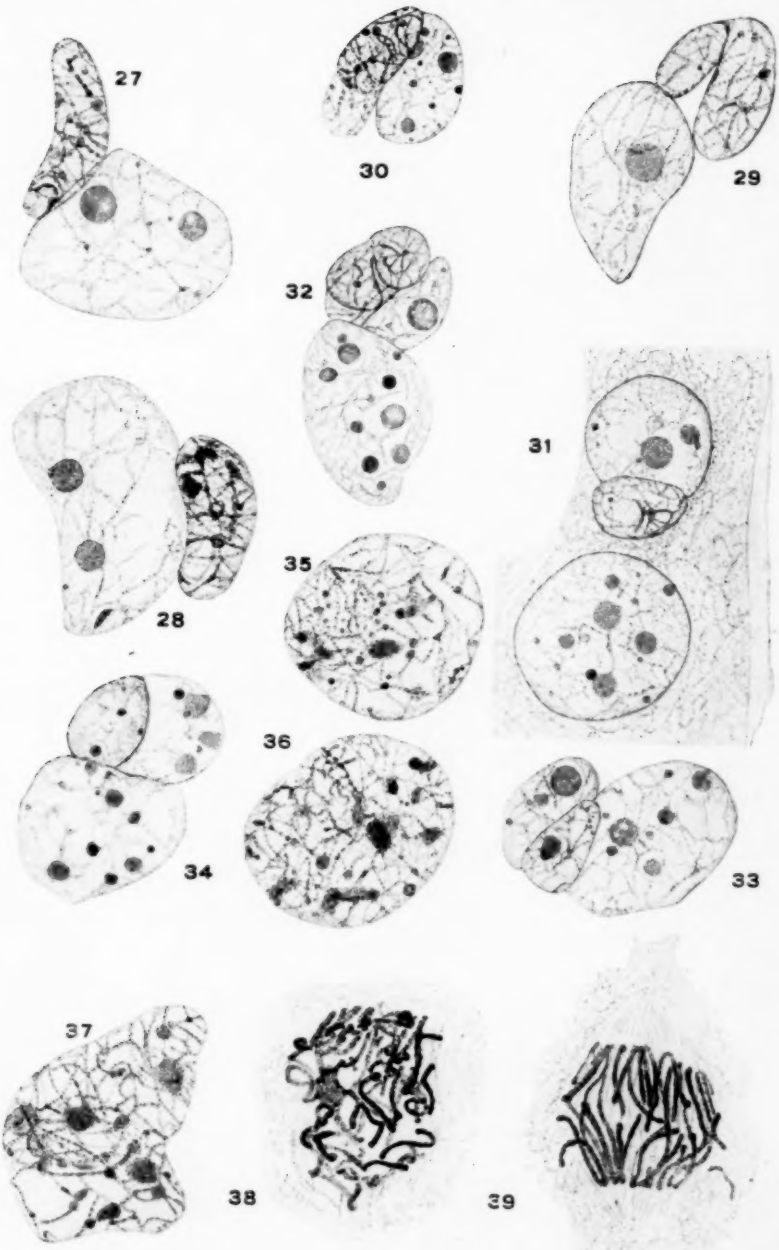

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